Revision of Homalomitrinae subfam. n. (Diptera: Sphaeroceridae), with the description of a new genus and three new species

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Taxonomy, Sphaeroceridae, Homalomitrinae, new subfamily, *Homalomitra*, redefinition, *Sphaeromitra*, new genus, new species, redescriptions, key, relationships, Neotropical region

Abstract. A new subfamily Homalomitrinae is established for two enigmatic Neotropical genera, *Homalomitra* Borgmeier, 1931 and *Sphaeromitra* gen. n. which are diagnosed on the basis of newly discovered characters. All available specimens of the group are revised. Two new species of *Homalomitra*, *H. antiqua* sp. n. (Costa Rica, Brazil) and *H. tenuior* sp. n. (female only; Colombia, Ecuador) are described and the remaining species of the genus, *H. ecitonis* Borgmeier, 1931 (type species, Brazil) and *H. albuquerquei* Mourgués-Schurter, 1987 (Costa Rica) are redescribed. A key to *Homalomitra* species is given. *Sphaeromitra inepta* gen. et sp. n. is described from Peru. Phylogenetic relationships of Homalomitrinae, both its genera and all species included are discussed.

INTRODUCTION

Homalomitra Borgmeier, 1931 (type species Homalomitra ecitonis Borgmeier) was described on the basis of a single very unusual-looking female specimen taken in a group of army ants in Brazil. The genus was known only from the type specimen until Mourgués-Schurter (1987) discovered a few additional specimens in the Museu de Zoologia da Universidade de São Paulo, and described a new species, Homalomitra albuquerquei, from Costa Rica. Homalomitra species are bizarre-looking, with all tarsal segments conspicuously dilated and dorsoventrally compressed, and with a very broad, dorsally flattened head. Perhaps because of this aberrant appearance, opinions have been divided about the taxonomic position of Homalomitra, with some authors (Richards, 1967, 1968; Hackman, 1969) suggesting a relationships with the Sphaerocerinae, and others linking it to the Limosininae (Mourgués-Schurter, 1987).

When, recently, we obtained several additional specimens (including some very different from the true *Homalomitra*) from samples collected in Malaise traps in various parts of Neotropical Region, we decided to revise all available material referable or similar to this genus and to redescribe it in detail to solve its systematic position. Our study of *Homalomitra* specimens not only revealed three unnamed species and a new peculiar genus, but enabled redefinition of the group on the basis of new characters, and elucidation of its relationships, eventually leading to the conclusion that it is necessary to establish a new subfamily for this group.

MATERIAL AND METHODS

All available material belonging to the group under study has been examined. It is deposited in the following collections: DEBU – Department of Environmental Biology, University of Guelph (Canada);

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INBC – Instituto Nacional de Biodiversidad, San José (Costa Rica); MZSP – Museu de Zoologia, Universidade de São Paulo (Brazil); SMOC – Silesian Museum, Opava (Czech Republic); USNM – U.S. National Museum of Natural History, Washington (USA). The specimens studied by Mourgués-Schurter (1987) were re-examined but they were mostly in exceptionally poor condition. Some specimens were dried from ethanol and mounted on points in the course of our study. Abdomens of the majority of specimens were detached, cleared, dissected and after examination all dissected parts put into coalesced plastic tubes containing glycerine and pinned below the respective specimens; this is indicated by the abbreviation "genit. prep." in text. The presentation of label data is strictly verbatim for all type and other specimens examined, with only the name of country added in certain cases.

The two most different species of *Homalomitra*, *H. ecitonis* (the type species) and *H. antiqua* sp. n., are described in full; other species of the genus are compared with these and their descriptions abbreviated accordingly. Because many specimens were in poor condition, chaetotaxy and certain structures sometimes had to be partly reconstructed in the figures, usually on the basis of the other side of the same specimen or other individual if available.

Morphological terminology essentially follows that used in recent papers by the senior author (e.g. Roháček, 1991) except for some terms pertaining to the male hypopygium. The "hinge" hypothesis of the origin of the eremoneuran hypopygium (see Zatwarnicki, 1996) was accepted in this study and, consequently, the following changes of terms of the male genitalia against the above-quoted paper are to be listed (new terms first): ejacapodeme – ejaculatory apodeme, epandrium – periandrium, medandrium – intraperiandrial sclerite, phallapodeme – aedeagal apodeme.

Abbreviations of morphological terms used in text and/or figures:

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A_1
             anal vein
                                                         mt,
                                                                      mid basitarsus
             acrostichal (seta)
                                                                      notopleural (seta)
ac
                                                         npl
              basal medial cell
                                                                      ocellar (seta)
                                                         oc
br
             basal radial cell
                                                                       external occipital (seta)
                                                         occe
C
                                                                       internal occipital (seta)
              costa
                                                         occi
                                                                      orbital (seta)
ce
           - cercus
                                                         ors
             costagial (seta)
                                                                      postalar (seta)
                                                         pa
                                                                       postgonite (= paramere or gonostylus
Cs<sub>2</sub>, Cs<sub>3</sub>
             2nd, 3rd costal section
                                                         pg
CuA<sub>1</sub>
                                                                       of North American authors)
              posterior cubital cell
cup
                                                         pha
                                                                      phallapodeme
cx_1
             fore coxa
                                                         phu
                                                                      posthumeral (seta)
dc
             dorsocentral (seta)
                                                                      phallophore
                                                         pp
dm
             discal medial cell
                                                                       propleural (= proepimeral) (seta)
                                                         ppl
              discal medial-cubital (= posterior, t<sub>p</sub>)
                                                         PTP
                                                                       pteropleuron (= anepimeron)
dm-cu
                                                                       pteropleural (= anepimeral) (seta)
              cross-vein
                                                         ptpl
dp
             distiphallus
                                                                       first radial cell
                                                         r,
ea
              ejacapodeme
                                                         R,
                                                                       1st branch of radius
                                                        R_{2+3}
              epandrium
                                                                      2nd branch of radius
ep
f_1, f_2, f_3
              fore, mid, hind femur
                                                         R_{4+5}
                                                                      3rd branch of radius
                                                                      radial-medial (= anterior, t<sub>p</sub>)
             genal (seta)
g
                                                         rm
              gonostylus (= surstylus)
                                                                       cross-vein
gs
              humeral (= postpronotal) (seta)
                                                         rm\dm-cu -
                                                                      section between rm and dm-cu on M
hu
hy
              hypandrium
                                                         S2-S10 -
                                                                      abdominal sterna
              intra-alar (seta)
                                                         sa
                                                                      supra-alar (seta)
ia
ifr
              interfrontal (seta)
                                                                       scutellar (seta)
                                                         sc
M
              media
                                                         Sc
                                                                       subcosta
ma
              medandrium
                                                         STP
                                                                       sternopleuron (= katepisternum)
             maxillary palp
                                                         stpl
                                                                       sternopleural (= katepisternal) (seta)
mp
MSPa
              mesopleuron (= anepisternum),
                                                         T1-T10 -
                                                                       abdominal terga
                                                                      fore, mid, hind tibia
              anterior part
                                                         t_1, t_2, t_3
              mesopleural (= anepisternal) (seta)
mspl
                                                         νi
                                                                       vibrissa
              mesopleuron (= anepisternum),
                                                                      outer vertical (seta)
MSPp
                                                         vte
              posterior triangular part
                                                         vti
                                                                    - inner vertical (seta)
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Subfamily Homalomitrinae subfam. n.

Type genus: *Homalomitra* Borgmeier, 1931. Other genera included: *Sphaeromitra* gen. n. (described below).

DIAGNOSIS. Sphaeroceridae of strange appearance, externally with some apparent similarity to members of the subfamily Sphaerocerinae but actually more closely related to Limosininae (see phylogenetic considerations below). The subfamily can be diagnosed as follows: (1) Head (Fig. 29) enlarged and, particularly, broadened. (2) Frons very broad, flattened or even concave, rarely slightly convex. (3) Ocelli always absent. (4) Frontal triangle absent or poorly developed. (5) Frontal setae very reduced, at most with small and short 1 oc, 1-2 setae in dorsal part of occiput (?occe, ?vte, ?vti) and 1-2 ors or frons completely without macrosetae. (6) vi distinct; g reduced or absent. (7) Antenna long, with scape (Figs 29, 30) strikingly enlarged. (8) Arista apical, ciliate. (9) Mesopleuron (Figs 25, 32) divided and its posterior part weakly sclerotized or completely membranous (Fig. 52). (10) Mesopleuron, pteropleuron, sternopleuron and sometimes also posterior part of hypopleuron (meron) with microsetulae; macrosetae on pleural part of thorax sometimes present, sometimes absent completely. (11) Legs robust compared to thorax. (12) Male f, and t, with (at least) short spine-like setae ventrally (Fig. 31); all other femora and tibiae (in female also fore tibiae) without macrosetae. (13) All tarsi with dilated and dorsoventrally flattened segments. (14) Claws inserted in deeply excavated apical tarsal segment (Fig. 4). (15) Veins M and CuA, not reaching wing margin. (16) Cells bm and cup not developed. (17) A, very reduced. (18) Alula very small and narrow. (19) Male S6, S7 and S8 coalesced together. (20) Epandrium (Figs 12, 63) simple, without ventrolateral cleft. (21) Anal fissure of epandrium small. (22) Hypandrium simple, V-shaped in dorsal view, without rod-like apodeme. (23) Subanal plate (reduced cerci) completely fused with epandrium (no boundary beween original cerci and epandrium visible. (24) Medandrium simple but distinct. (25) Gonostylus unilobate, with at least some micropubescence. (26) Distiphallus (Figs 37, 59) short and robust, largely membranous but with complex slender internal sclerites arising from heavily sclerotized central "core" lying in its proximal part. (27) Postgonite robust, with various projections and keels. (28) Ejacapodeme very reduced or absent. (29) Spermathecae (1+1) black, spherical, with heavily sclerotized terminal part of duct (Figs 26, 67). (30) Female T10 and S10 without micropubescence. (31) Female cerci with rich setosity but without micropubescence (Fig. 17).

Discussion. The above diagnosis includes both plesiomorphic and highly apomorphic characters as well as features of uncertain interpretation (e.g. 8, 10, 19, 21, 27, 29). Characters 15, 16, 18, 20, 22, 24, 25 are distinctly plesiomorphic within the Limosininae but some of them (15, 16) synapomorphic for the Homalomitrinae + Limosininae clade (see cladogram, Fig. 68). In contrast, characters 1–7, 9, 11–14, 17, 23, 26, 28, 30–31 are clearly apomorphic and demonstrate the monophyly of the new subfamily. Consequently, Homalomitrinae is a well characterized group, sharply delimited from all other subfamilies of Sphaeroceridae.

The unusual external appearance of *Homalomitra* Borgmeier, 1931 misled the previous authors (Borgmeier, 1931; Richards, 1968; Hackman, 1969) to associate it with the unrelated subfamily Sphaerocerinae. The new genus *Sphaeromitra*, described below, is yet more similar to certain sphaerocerine genera, resembling them also in the structure of epistoma, reduced setosity and abdominal sterna. This is, however, only a striking

homoplasy and not a reflection of the relationships of Homalomitrinae with Sphaerocerinae.

The subfamily Homalomitrinae includes only two Neotropical genera which are keyed and treated in detail below.

Key to genera of Homalomitrinae

- Frons with 3 prominent tubercles (Figs 53, 55); scapes short, medially separated (Fig. 55); epistoma expanded dorsally and forming deep antennal pits (Figs 52, 55); mesonotum without macrosetae (Fig. 53); wing short, with strongly reduced veins (M, cells br, dm and all cross-veins absent) and without costagial seta (Fig. 56); preabdominal sterna reduced and male S5 absent (Fig. 58)
 Sphaeromitra gen. n.

Genus Homalomitra Borgmeier, 1931

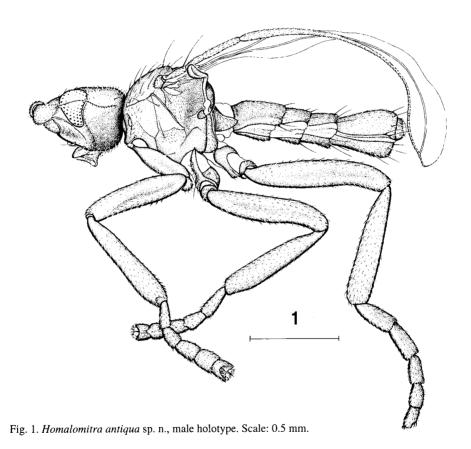
Homalomitra Borgmeier, 1931: 32; Richards, 1967: 6 (catalogue); Mourgués-Schurter, 1987: 113. Type species: *Homalomitra ecitonis* Borgmeier, 1931: 32 (original designation).

Diagnosis. (1) Head (Fig. 29) large, broader than thorax, dorsally flattened. (2) Frons very broad (Figs 2, 29), anteriorly broadly rounded, flat. (3) Frontal triangle and ocelli absent. (4) Interfrontalia and ocellar triangle reduced but still visible. (5) Gena (Fig. 32) narrowed and high (deep); occiput (and postgena) enlarged. (6) Frontal setae strongly reduced, only 1 oc, 1–2 setae in dorsal part of occiput (?occe, ?vte, ?vti) and 1–2 ors discernible; 4–6 ifr reduced to microsetae. (7) Vibrissal angle reduced; face strongly oblique. (8) vi distinct; g reduced or absent. (9) Antennal scapes extremely enlarged (larger than pedicel or 1st flagellomere) and meeting dorsomedially (Fig. 2); pedicel subconical, as long as or longer than 1st flagellomere. (10) Arista apical, with medium long ciliation. (11) Epistoma reduced, mouth opening relatively small. (12) Maxillary palp very small and slender (Fig. 3).

(13) Thorax narrow (Fig. 29), short but high; scutellum small and narrow. (14) Thoracic chaetotaxy rich on mesonotum (setae long but very thin) but more or less reduced on pleuron. (15) 1 hu, 2 short posthumerals, 2 npl (anterior and posterior), 1 sa, 1 pa. (16) 1 very long ?ia. (17) 3–5 dc (1–3 presutural); ac variable. (18) 2 sc, apical distinct, lateral reduced to microseta. (19) Mesopleuron divided (Fig. 25), with separate posterior triangular part being often weakly sclerotized and less pigmented. (20) Mesopleuron, pteropleuron, sternopleuron and sometimes also posterior part of hypopleuron with microsetulae; primitively (H. antiqua sp. n., see Fig. 1) with 1 ppl, 1 mspl, 1 ptpl and 2 stpl setae in addition. (21) Legs long and robust (Fig. 1), with large fore coxa; mid basitarsus relatively short. (22) Male f, and t, (Fig. 31) with ventral short spine-like setae; all other femora and tibiae (in female also fore tibiae) without macrosetae. (23) All tarsi with dilated and dorsoventrally flattened segments. (24) Claws inserted in deeply excavated apical tarsal segment (Fig. 4). (25) Wing (Figs 6, 41) long and narrow, with very long marginal cilia. (26) C with long costagial seta. (27) C moderately to strongly dilated in Cs₂ and produced beyond apex of R₄₊₅. (28) Index Cs₂: Cs₃ always higher than 1.5. (29) Cell br strongly narrowed and cross-vein r-m extremely short; cell dm very long and narrow. (30) Apical sectors of M and CuA_1 long but not reaching wing margin. (31) bm and cup cells not developed. (32) A_1 reduced, strongly bent basally. (33) Alula very small and narrow. (34) Haltere unusually long (Fig. 32).

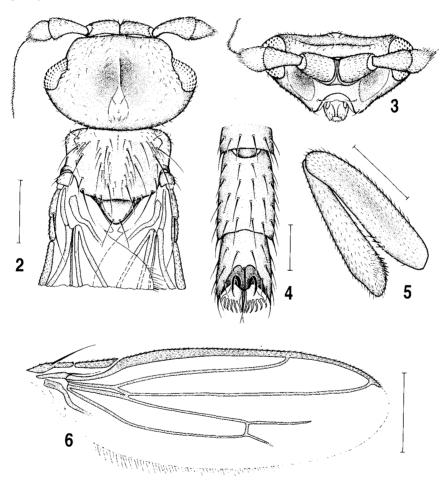
(35) Abdomen long (Figs 7–10), both preabdominal terga and sterna large (including S2). (36) Preabdominal terga and sterna densely microsetose and with long setae at posterior margins. (37) Male S5 (the largest sternum, Fig. 38) very long but simple, without posterior modifications. (38) Male S6, S7 and S8 coalesced together. (39) Epandrium long but simple (Fig. 12), without ventrolateral cleft. (40) Anal fissure of epandrium small, rounded. (41) Hypandrium simple, V-shaped in dorsal view. (42) Subanal plate (reduced cerci, Fig. 13) completely fused with epandrium, with a narrow ventromedial cleft. (43) Medandrium simple but relatively broad. (44) Gonostylus unilobate, with dense micropubescence on external side. (45) Phallophore (Fig. 37) of complex structure and with small epiphallus. (46) Distiphallus short and robust, largely membranous but with complex internal sclerites arising from heavily sclerotized central "core" lying in its proximal part. (47) Postgonite robust, as long as distiphallus, with various projections and keels. (48) Ejacapodeme very reduced (Fig. 14).

(49) Female postabdomen with T6 and S6 (Figs 9, 10) similar to preceding sclerites both in shape and chaetotaxy but yet longer. (50) T7 and S7 (Figs 17, 19) conspicuously

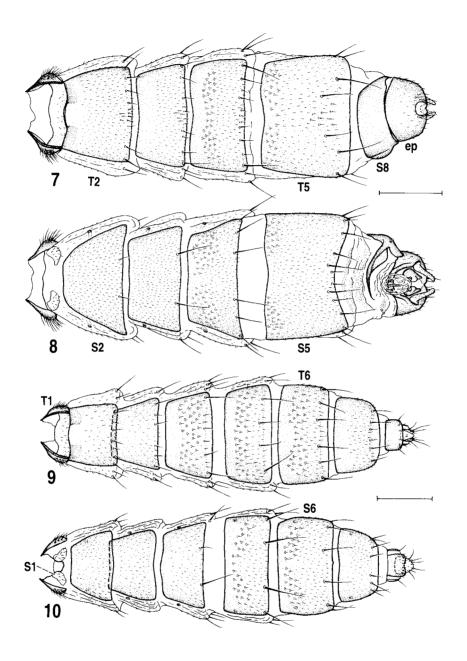


broader than T8 and S8. (51) T8 small, with reduced number of setae. (52) S8 narrower than T8, simple, with dense micropubescence besides usual setae. (53) Spermathecae (1+1) black (Fig. 26), more or less sphaerical, with a crown of tubercles or projections surrounding base of sclerotized part of duct. (54) T10 and S10 without micropubescence (Figs 17–19). (55) Female cerci (Fig. 17) with rich setosity but without micropubescence.

Discussion. This distinctive genus is easily recognizable by a peculiar combination of plesiomorphic (with respect to the sister-group *Sphaeromitra* gen. n.; see characters No. 4, 6, 11, 14, 15, 17, 18, 28–30, 32, 35–37, 49, 50) and highly apomorphic characters (5, 7, 9, 12, 16, 25–27, 34, 45, 53). It differs from *Sphaeromitra* gen. n. in all these features, but at least the following should be stressed as the most characteristic: head with conspicuously shortened (narrowed) gena, expanded occiput (plus postgena) and strongly oblique face making, together with small mouth opening, lateral as well as frontal outline of head



Figs 2–6. Homalomitra antiqua sp. n., male holotype. 2 – head and thorax dorsally; 3 – head frontally; 4 – apical segments of hind tarsus; $5 - f_1$ and t_1 anteriorly; 6 – wing. Scales: 4 - 0.1 mm; 6 - 0.5 mm; others – 0.3 mm.



Figs 7–10. *Homalomitra antiqua* sp. n., male holotype (7, 8), female allotype (9, 10). 7 – male abdomen dorsally; 8 – ditto ventrally; 9 – female abdomen dorsally; 10 – ditto ventrally. Scales: 0.3 mm.

strikingly triangular; broad frons peculiarly flattened and sometimes even concave; vibris-sal angle reduced; antenna with extremely enlarged, densely setulose scape, subconical pedicel and relatively small 1st flagellomere; unusually small palpus; rich, long and fine mesonotal setae with particularly conspicuous ?intra-alar seta; divided mesopleuron with posterior triangular area; large fore coxa; long wing with relatively primitive (in comparison with most genera of Limosininae) venation but with apomorphic long costagial seta, long marginal ciliation and thickened C; haltere strikingly long; large flat preabdominal terga and sterna; phallophore of complex structure (not compact); spermathecae with a crown of projections surrounding base of duct.

Borgmeier (1931) first noted that the head of *Homalomitra ecitonis* resembles that of certain species of Sphaerocerinae. Richards (1967) placed the genus behind *Sphaerocera* (s. lat.), and later (Richards, 1968) considered it to be related to that genus (= i.e. to Sphaerocerinae as presently understood). Hackman (1969), following Richards's (1968) opinion, included *Homalomitra* in the Sphaerocerinae. Only recently Mourgués-Schurter (1987: 116) correctly recognized that *Homalomitra* cannot belong to Sphaerocerinae because of lack of synapomorphic features of this subfamily, and suggested it is more similar to "subfamilia Leptocerinae" (= Limosininae).

The genus includes 4 Neotropical species, viz. *Homalomitra antiqua* sp. n. (Costa Rica, Brazil), *H. tenuior* sp. n. (Colombia, Ecuador), *H. ecitonis* Borgmeier, 1931 (Brazil) and *H. albuquerquei* Mourgués-Schurter, 1987 (Costa Rica) which are keyed and (re)described below. All these species are probably associated with New World army ants of the genus *Eciton* (Formicidae: Ecitoninae).

Key to species of Homalomitra

- 3 Body dark ochreous with greyish tinge, legs and wing pale ochreous; C less dilated, cell r₁ of about half width of C in Cs₂ (Fig. 41); 7–8 short ventral spines on male f₁ and 8 similar spines on t₁ (Figs 31, 32); male S5 shorter and S6 with a pair of small digitiform processes ventromedially (Fig. 38); gonostylus (Fig. 36) only partially micropubescent on outer side; postgonite (Fig. 39) complex, with a number of keels and projections; female postabdomen as in Figs 43–44 H. ecitonis Borgmeier
- Body black-brown, legs and wings brown. C extremely dilated, almost completely filling cell r₁ (Fig. 46); 3-4 short ventral spines on male f₁ and 6 similar spines on t₁ (Figs 47, 51); male S5 longer and S6 ventromedially thickened and posteriorly emarginate (Fig. 50); gonostylus (Fig. 48) externally

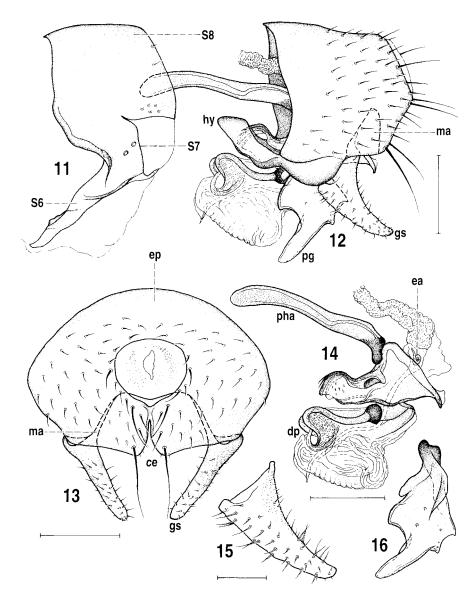
Homalomitra antiqua sp. n.

DESCRIPTION, Male (Fig. 1). Total body length 2.34 mm. General colour ochreous vellow, only head darker, partly (mainly dorsally) brown. Head (Figs 2, 3) distinctively shaped, broader than thorax, dorsally flattened to slightly concave on frons, in lateral and anterior views subtriangular. Frons very wide, dull, brown except for the orange-ochreous ocellar triangle and anterior margin (Fig. 2). Ocelli absent. Frontal triangle not delimited; the slightly depressed areas between orbits and ocellar triangle with sparse, silvery-grey microtomentum. Occiput medially with oval orange-ochreous spot wider than ocellar triangle. Cephalic setae strongly reduced but some of macrosetae (although only slightly longer and thicker than other setulae on frons) discernible: 2 pairs of exclinate setae in dorsal part of occiput (?occe and ?vte), 1 distinct oc pair and 1-2 microsetulae behind it besides several other microsetulae at posterior margin of ocellar triangle, 1-2 ors and several (4-5) fine ifr. There are numerous fine setulae scattered on dorsal side of head, particularly anteriorly, on orbits and on occiput (postocular area). Lateral side of head with large, sharply separate and pale ochreous postgenal-occipital area, reduced (narrowed) but high gena forming a perpendicular brown stripe, and with extended ochreous face (prefrons) having shallow lateral concavities (Fig. 1). One distinct but short vi at anteroventral margin of gena (vibrissal angle not developed) and another seta (?g) behind it apart from fine setulae on ventral part of gena and boundary between gena and occiput. Epistoma small, not expanded. Eye small (its longest diameter about as long as genal height), convex, subtriangular in lateral view (Fig. 1). Antenna (Figs 2, 3) with conspicuously enlarged and densely setulose scape, relatively long conical and similarly setulose pedicel, and with egg-shaped 1st flagellomere having fine long cilia on apex. Arista densely and finely ciliate but its length is unknown (apical parts broken off in all specimens examined).

Thorax (Figs 1, 2) narrow, white-yellow, mesonotum with two darker ochreous areas separated by pale acrostichal area and anteriorly with a very narrow brown medial stripe almost reaching middle of mesonotum. Thoracic setae long but fine. There are 4-5 (2-3 presutural) dc (posterior the longest) and 3-4 unusually laterally shifted presutural ac with 2nd pair particularly long; postsutural ac small including the prescutellar pair. Humeral callus with 1 short hu and numerous setulae; 2 npl (anterior much longer than posterior); 2 posthumerals; 1 very long ?ia; 1 short sa and 1 very long pa; 2 additional short prescutellar setae between pa and dc. Scutellum small, yellow-white, rounded triangular, with 1 long and thin apical sc and 1 minute lateral sc. Pleural part pale ochreous-yellow to whiteyellow. Propleuron with numerous fine setulae and 1 long ppl situated above base of fore coxa. Mesopleuron subdivided into 2 triangular parts (as characteristic for *Homalomitra*); its anterodorsal corner with several setulae and dorsal corner of its posterior part with 1 distinct mspl seta. Sternopleuron with 1 anterior stpl dorsally and 1 short stpl ventrally above mid coxa in addition to fine microsetulae covering its dorsal third. Posterior part of hypopleuron and pteropleuron also with dense fine microsetulae and the latter with 1 longer ptpl seta in addition.

Legs (Figs 1, 5) long and stout compared to small thorax, pale yellowish ochreous and finely densely setulose. cx, very large. f, ventrobasally with 3 short black setae and t, (Fig.

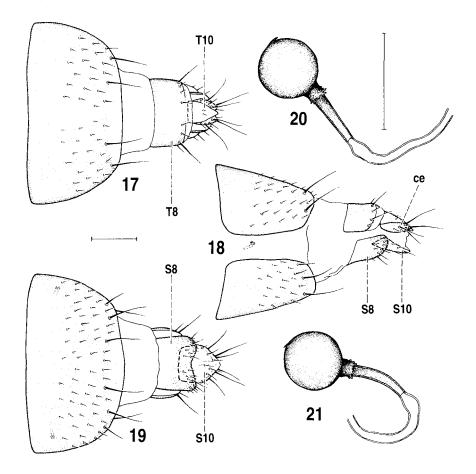
5) with 2 ventral rows of dense black spinulae in apical fourth and with 2 short preapical anterodorsal fine setae; f_2 without peculiarities and t_2 with only 1 small ventroapical seta; f_3 and t_3 also with simple, though somewhat longer, pilosity. All tarsi with conspicuously dilated segments, only fore and mid basitarsus slightly less thickened. Last tarsal segments



Figs 11–16. Homalomitra antiqua sp. n., male holotype. 11-86, S7 and S8 laterally; 12- genitalia laterally; 13- ditto caudally (aedeagal complex omitted); 14- aedeagal complex laterally (postgonites omitted); 15- gonostylus sublaterally (widest extension); 16- postgonite laterally. Scales: 15-0.05 mm; others -0.1 mm.

with apices deeply excavated (Fig. 4) and with claws inserted in this hole. Mid basitarsus relatively short, less dilated than following segments; ratio t_2 : $mt_2 = 2.60$. Hind basitarsus robust, less flattened but thicker than 2nd tarsal segment, both with posterior brush of dense hairs.

Wing (Fig. 6) long, narrow, with both veins and membrane ochreous brown. C with 2 usual costal breaks and basally provided with thin and very long costagial seta. C relatively strong but not enormously dilated, reaching somewhat beyond apex of R_{4+5} . Sc short and reduced, vanishing in membrane. R_1 short. R_{2+3} relatively long, slightly sinuate and apically strongly curved to C. R_{4+5} almost straight except apical ninth which is distinctly bent up to C. Cross-vein r-m very shortened and situated in basal fourth of wing. Discal cell (dm) very long and narrow, with long process of M beyond dm-cu and a shorter process of CuA_1 . A_1 strongly reduced with indistinct apex. Posterior wing margin provided with unusually long cilia (observed in only proximal two-thirds of wing; ?lost in the rest of margin). Alula small and narrow. Wing measurements: length 2.38 mm, width 0.79



Figs 17–21. *Homalomitra antiqua* sp. n., female allotype. 17 – apex of postabdomen dorsally; 18 – ditto laterally; 19 – ditto ventrally; 20, 21 – spermathecae. Scales: 0.1 mm.

mm, Cs_2 : $Cs_3 = 1.89$, rm\dm-cu : dm-cu = 9.27. Haltere unusually long and slender, yellow-white, with very thin stem and flattened, spoon-shaped knob.

Abdomen pale ochreous-yellow, relatively narrow (Figs 7, 8), dorsoventrally flattened. T1 membranous dorsomedially; its lateral sclerotized parts with long and dense hairs. S1 preserved as 2 small, weakly sclerotized but setulose remnants in front of S2. Other preabdominal terga and sterna large, broad, with macrosetae only at posterior margins of T2–T5 and S2–S5. T2 longer than T3 or T4. T5 is the largest abdominal tergum; preabdominal sterna similar to associated terga (see Fig. 8), i.e. S5 the largest. Spiracles 2–5 situated in membrane between relevant terga and sterna. Postabdominal sterna (S6–S8) fused together, i.e. synsternite S6+7 fused with S8 (see Figs 8, 11) and strongly asymmetrical. S6 positioned mainly ventrally, S7 left laterally and S8 dorsally but boundary between them hardly recognizable; narrow ventral part of S6 simple. Two usual spiracles (6 and 7) situated in S6+7; S8 with a group of microsetae at posteroventral margin and with 2 setae left posteriorly (Fig. 11). There are also 2 spiracles close to each other in ventral membrane on right side in front of epandrium (Fig. 8).

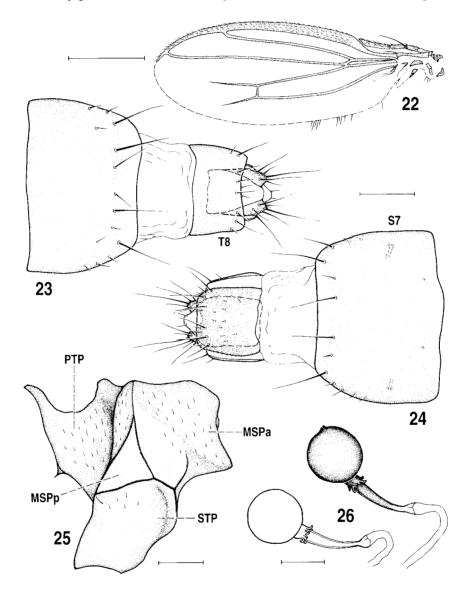
Genitalia (Figs 12-16). Epandrium (Figs 12, 13) relatively long and broad, with dense short setulae except for 2 pairs of long setae around anal fissure and 1 (longest) pair on reduced cerci forming subanal plate. Anal fissure small, subcircular; subanal plate rather large, with narrow ventromedial cleft (Fig. 13). Hypandrium (Fig. 12) robust, V-shaped, without anteromedial apodeme; its lateral arms fused posteriorly to epandrium. Medandrium (Fig. 12, 13) simple, connected with posterodorsal corner of gonostylus. Gonostylus (Figs 13, 15) relatively narrow, tapered apically and slightly bent in lateral view; all surfaces shortly setulose, its posterodorsal surface with a microtomentose area. Internal genitalia relatively robust (Fig. 14). Phallapodeme simple, rod-like, without dorsal keel. Phallophore with small posteroventral process (epiphallus) and complex anterodorsal end with fine projections and inner structures. Distiphallus largely membranous but with heavily sclerotized central core near base from which a pair of strongly sinuous filaments emanates anterodorsally. Postgonite (Fig. 16) large, complex, with a finger-like apical process and several teeth and keels both anteriorly and posteriorly. Ejaculatory duct passes through the whole aedeagus and bears a reduced ejacapodeme (Fig. 14) near posterior margin of basiphallus.

Female. Similar to male unless mentioned otherwise. Total body length 2.02–2.18 mm. f_1 and t_2 without special armature ventrally. t_2 : mt_2 = 2.76–2.94. Wing measurements: length 1.79–2.06 mm, width 0.63–0.71 mm, Cs_2 : Cs_3 = 1.71–2.38, rm\dm-cu : dm-cu = 7.82-8.33.

Abdomen (Figs 9, 10). Preabdomen similar to that of the male but narrower and longer, and more broadened in posterior half (5th and 6th segments are the widest). Lateral parts of T1 less densely setulose. S2 and S3 without macrosetae; otherwise sclerites of 2nd–4th segments similar to those of male. T5 and S5 essentially shorter and more transverse than in male.

Postabdomen. 6th segment similar to preceeding but longer (Figs 9, 10). 7th segment (Figs 17–19) distinctly narrower than the 6th but resembling the latter in chaetotaxy and structure of sclerites. T7 (Fig. 17) relatively broad, with numerous small setulae on disc and 2 pairs of longer setae at posterior, pale pigmented, margin. S7 (Fig. 19) similar to T7 but with setulae more numerous and 3 pairs of longer posterior setae. T8 (Fig. 17) small,

considerably narrower than T7 but transverse and with setae restricted to posterior margin, the lateral setae longest. S8 (Fig. 19) longer but narrower than T8, medially shallowly emarginate, with short setulae posteriorly and densely microtomentose in posterior two-thirds. Internal vaginal structures largely membranous, with a ventral, poorly visible ring. Two accessory glands on slender (half of spermathecal duct's diameter) and long, smooth



Figs 22–26. Homalomitra tenuior sp. n., female holotype. 22 – wing; 23 – apex of postabdomen dorsally; 24 – ditto ventrally; 25 – right pleural sclerites laterally; 26 – spermathecae. Scales: 22 – 0.5 mm; 26 – 0.05 mm; others – 0.1 mm.

ducts. Spermathecae (1+1) black, almost perfectly spherical (Figs 21, 22); each with 1 spine-like process on top and with a long, sclerotized, black-brown terminal part of duct armed with a subterminal crown of short pale brown spines and tubercles. T10 (Fig. 17) simple, very narrow, pale, posteriorly pointed, with a pair of small central setulae. S10 (Fig. 19) distinctly broader than T10, with several setulae along posterior margin but without micropubescence. Cerci relatively small, slender but hardly projecting beyond apex of T10; each cercus with 4 longer setae (apical, dorsopreapical, ventropreapical and lateral) and a few shorter setulae but without microtomentum.

Type Material: Holotype ♂, "Costa Rica: San José, Zurquí de Moravia, 10.05°N, 84.02°W, 1.–15.vi.1993, P. Hanson [leg.], Malaise trap, 1600 m". Allotype ♀ with the same label-data but dated "vi.1992". Holotype male with left mid and hind legs missing; its left wing and abdomen detached, the latter with genitalia removed and dissected and all parts mounted in plastic tube in glycerine pinned below the specimen (DEBU). Female allotype with genit. prep. and deposited in INBC. Paratypes 2♀, "Brazil: Cruzeiro do Sul, Acre ii.1973, arm. luminosa, A.P. do Prado leg.". Both specimens dried from ethanol and mounted on pinned triangular cards (MZSP, SMOC).

ETYMOLOGY. The species is named "antiqua" (Lat. = antique, ancient; an adjective in nominative singular) because it retains numerous ancient (plesiomorphic) features.

DISTRIBUTION. Costa Rica, Brazil.

Biology. Holotype male and allotype female were caught in Malaise traps, both in June (in two subsequent years). Both female paratypes from Brazil were collected in a light trap in February.

Discussion. H. antiqua sp. n. represents the sister-group to all remaining species of the genus Homalomitra because it lacks their apomorphic features. It retains a number of plesiomorphic characters in thoracic chaetotaxy (additional prescutellar setae between pa and dc; long apical sc; presence of 1 ppl, 1 mspl, 1 ptpl and 1 stpl); shape and structure of the male S6 (simple and slender ventromedially) and the female T7 and S7 (large, covered with dense setulae). H. antiqua sp. n. is also characterized by longer and narrower wings, different armature of the male f_1 and f_1 and distinctive male genitalia (e.g. slender gonostylus, shape of postgonite and spermathecae).

Two females of this species were recorded by Mourgués-Schurter (1987) under *H. ecitonis*; they are included in the type series of *H. antiqua* sp. n. as paratypes (see type material).

Homalomitra tenuior sp. n.

Description. Male unknown. Female most resembling that of *H. ecitonis* but differing as follows. Total body length 1.98–2.10 mm. General colour distinctly lighter than in *H. ecitonis*, yellowish ochreous to whitish yellow, without greyish tinge, although this may partly be due to certain immaturity of the type specimens. Head somewhat more flattened and lower than in *H. ecitonis*, with shallowly concave frons (as in *H. antiqua* sp. n.). Frons, vertex and dorsal part of occiput pale brown, except for orange-yellow anterior frontal margin, very narrow interfrontalia, narrow ocellar triangle and convex occipital spot behind ocellar triangle. Cephalic chaetotaxy similar to that of *H. ecitonis* but oc shorter, only slightly longer and thicker than setulae in two rows behind them; 1 ors longer and clearly recognizable from 2–3 shorter orbital setulae; 5–6 ifr setulae inserted on pale, well delimited interfrontalia; frontal microsetulae longer. Frons dull, with whitish grey micropubescence, but long narrow ocellar triangle and occipital pale spot (broader than the

latter) behind it largely bare. Gena paler and lower than that of *H. ecitonis*; no g but setulae at ventral margin of gena more numerous, in 2 rows. Antenna with scape yet somewhat broader (not longer) than in *H. ecitonis*. Arista longer than antenna (its precise length cannot be recognized because of apices broken off) and with distinctly longer cilia than that of *H. ecitonis*.

Thorax. Mesonotum with similar colour pattern but paler than in *H. ecitonis*; humeral callus completely whitish yellow. Pleural part of thorax pale yellow, with some parts almost white and very weakly sclerotized (viz. posteroventral part of mesopleuron, anterior part of hypopleuron, anterior part of metanotum). Thoracic setae very similar to those of *H. ecitonis*, including short thickened apical sc. Anterior part of mesopleuron (see Fig. 25, MSPa) with large bare and less sclerotized posterior area, ventrally covering about half of the sclerite. Microsetae longer and less numerous on mesonotum; some further microsetulae are not only in dorsal part of sternopleuron but also in posterodorsal corner of hypopleuron. Pteropleuron convex and densely finely setulose.

Legs very long, with long and dilated tarsi, without special macrosetae, uniformly finely, relatively long (longer than in H. ecitonis) and densely haired. t_2 with 2–3 reduced ventropreapical setulae. Ratio t_2 : $mt_2 = 2.84-2.97$.

Wing (Fig. 22) long and narrow as in *H. ecitonis* but with C less thickened (its maximum width not larger than that of marginal cell r_1) and without bare and pale posterior margin in Cs_2 , i.e. C more similar to that of *H. antiqua* sp. n. Cell br distinctly narrower and discal cell (dm) somewhat longer than in *H. ecitonis*; apical sectors of M and CuA_1 of less different lengths. i.e. that of CuA_1 longer. Marginal cilia very long. Alula small but distinct. Haltere long, with white stem and somewhat darker, spoon-shaped knob. Wing measurements: length 1.63–1.81 mm, width 0.61–0.68 mm, $Cs_2 : Cs_3 = 2.53–2.94$, rm\dm-cu : dm-cu = 7.11–8.22.

Abdomen pale to whitish yellow. All preabdominal terga distinctly narrower, less transverse than in *H. ecitonis*. T2–T4 with short flattened setae in front of posterior margin; T5 with a pair of short setae only medially and laterally with 2 long setae. T1–T6 with microsetulae (less dense than in *H. ecitonis*). Sterna S2–S5 similar in shape to relevant terga but in contrast to those of *H. ecitonis* with very long setae (2 pairs on each sternum) becoming longer posteriorly and in S5 being almost as long as length of sternum. S2–S6 microsetulose but more sparsely than those of *H. ecitonis*.

Postabdomen (Figs 23, 24). To similar to T5 but narrower and with only 6 (3 pairs) long posterior setae being distinctly shorter than length of tergum. So resembling T6 in shape but with only 4 long posterior setae. T7 (Fig. 23) and S7 (Fig. 24) long and little transverse, with 4 long setae and several setulae in front of posterior margin. T8 smaller and narrower than T7 but broader than S8, very finely microtomentose in posterior third only. S8 distinctly narrower and with longer setae than that of *H. ecitonis* (Fig. 44), densely microtomentose. Spermathecae (1+1) more similar to those of *H. antiqua* sp. n. than those of *H. ecitonis*, ball-shaped, with more or less distinct terminal tubercle (Fig. 26); sclerotized part of duct longer than body of spermatheca but only two-thirds of it dark and its crown of distinctive curved digitiform tubercles distinctly removed from the insertion point of duct. T10 similar to that of *H. ecitonis*, somewhat more triangular, bare except for usual pair of dorsal setae. S10 longer and narrower than that of *H. ecitonis*, without

micropubescence but with a few marginal setulae. Cerci (Fig. 23) with relatively long and rich hair-like setae and also with some microsetulae.

Type Material: Holotype $\,^\circ$, "Colombia: Rio Ramposo, 28.vii.1964, V.H. Lee [leg.], light trap". Paratype $\,^\circ$, "Ecuador: Pastaze Cononaco, 30 May 1976, J. Cohen [leg.], at light". Both specimens with identification label "Homalomitra ecitonis Borg., det. S. Marshall '83", type label (red) "Homalomitra tenuior sp. n. $\,^\circ$, J. Roháček & S.A. Marshall det. 1997, Holotypus (or Paratypus respectively)" and with genit. prep. In the holotype left wing is also removed and placed in glycerine together with the abdomen. Both specimens deposited in USNM.

ETYMOLOGY. The species is named "tenuior" (Lat. = more slender, thinner; an adjective in nominative singular) because the costa and female abdomen are more slender than those of the related *H. ecitonis*. DISTRIBUTION. Colombia, Ecuador.

BIOLOGY. Both type females were taken in light trap; one in May, the other in July.

Discussion. The species seems to be somewhat intermediate between H. antiqua sp. n. and H. ecitonis. It resembles the former in having a simple (not strikingly dilated in Cs_2) costa, longer-haired arista and paler colouration of body; the latter by reduced thoracic chaetotaxy (short apical sc, pleural part of thorax without macrosetae) and similar shape and chaetotaxy of postabdomen. It is obviously closer to H. ecitonis as the shared features are apomorphic (see the phylogenetic considerations below). Differences between H. tenuior sp. n. and H. ecitonis are given in the key and description.

Homalomitra sp.

Homalomitra ecitonis, part (male): Mourgués-Schurter, 1987: 114, Figs 1-2.

MATERIAL EXAMINED: "Brazil: Nova Teutônia, 27°11′8″S, 52°23 W, iv.1953, 300–500 m, 28, Fritz Plaumann [leg.]" (MZSP). The specimens (1 immature, 1 dissected and some its parts mounted on slide) are associated with 2 workers of host ant (identified as "E. praed." = *Eciton praedator*). The specimens were originally preserved in ethanol; the immature male was dried and mounted on pinned triangular card during the course of this study. Of the other specimen, only one of each pair of legs, wing (all on 1st slide) and genitalia (on 2nd slide) are preserved; both identified by L. Mourgués-Schurter as *H. ecitonis*.

DISTRIBUTION. Brazil.

COMMENTS. The available material is inadequate for description although the above specimens probably either represent an unnamed species or are conspecific with *H. tenuior* sp. n. described from two females. Unfortunately, the external body features cannot be studied because of very poor condition of the immature male and because the relevant parts are mising on slides with remnants of the other male and, consequently, these specimens cannot be associated with *H. tenuior* sp. n. with certainty.

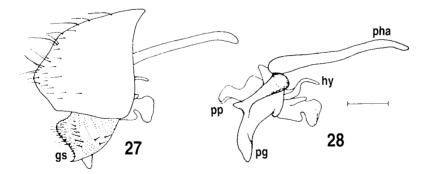
The non-dilated C and relatively long apical sector of CuA_1 suggest that the specimens belong to H. tenuior sp. n. Armature of f_1 and t_1 resembles that of H. ecitonis but, in contrast to the latter species, the specimens have only 4 short, thickened anteroventral setae on f_1 and 9 such setae on t_1 and all setae seem to be smaller than in H. ecitonis.

The genitalia (Figs 27–28, according to Mourgués-Schurter, 1987: Figs 1–2) are largely destroyed in the slide mount made by L. Mourgués-Schurter but the slender and relatively short phallapodeme is still visible and demonstrate that Figs 1–2 of Mourgués-Schurter (1987) were based on this specimen. While the postgonite is very similar to that of *H. ecitonis* (cf. Figs 28, 39), there is a distinct difference in the shape of phallapodeme, which is longer and has distinct dorsal keel in *H. ecitonis*.

Homalomitra ecitonis Borgmeier, 1931: 32; Richards, 1967: 6 (catalogue), 1968: 183 (note on taxonomic position); Hackman, 1969: 199 (classification); Steyskal, 1971: 376 (note on type material); Mourgués-Schurter, 1987: 114 (redescription).

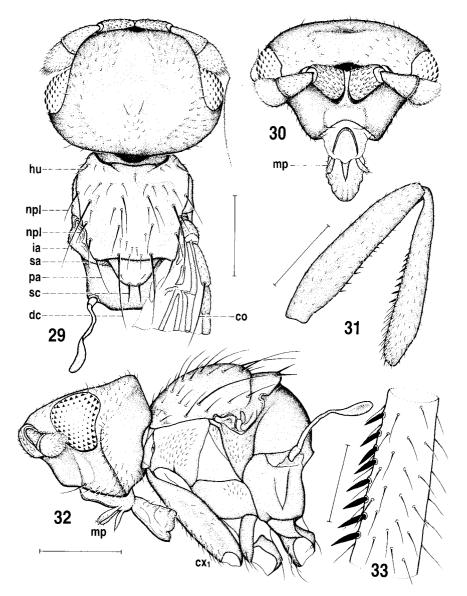
REDESCRIPTION. Male (new). Total body length cca 2.0 mm. General colour ochreous, with some greyish tinge, head distinctly darker than thorax or abdomen, brown to pale brown. Head (Figs 29, 30, 32) distinctly broader than thorax, subtriangular in profile, dorsally flattened. Frons broad, dull brown or with somewhat paler interfrontalia and oval area in its posterior half. Frontal triangle not visible; ocellar triangle indistinctly delimited. Ocelli absent. No distinct pale spot behind ocellar triangle. Cephalic setae very reduced, most of frons covered with microsetulae only. Frontal chaetotaxy: 1 pair of exclinate setae in dorsal part of occiput (?occe), 1 distinct oc pair (not recognized by Borgmeier 1931: Fig. 1) and several microsetulae behind it; 1 very reduced (hardly recognizable) ors plus several additional microsetulae on orbit; a row of very indistinct (4-6) ifr being hardly different from microsetulae laterally to them; numerous microsetulae mainly distributed on orbits, between orbits and interfrontalia and in postocular area. Lateral side of head with large, pale ochreous, postgenal-occipital area contrasting with darker brown gena. Gena high and narrow. Face extended, pale ochreous laterally, somewhat darker medially, with shallow lateral concavities. Vibrissal angle poorly developed but vi distinct. No g present; gena with several microsetulae at ventral margin; posterior margin of gena darkened and with a double row of setulae; a number of microsetulae also on ventral part of occiput. Epistoma small, not expanded dorsally. Eye small but convex, rounded triangular in lateral view (Fig. 32); its longest diameter about as long as genal height. Antenna with enlarged scape (only slightly smaller than in H. antiqua sp. n.), subconical pedicel (both densely setulose) and small, ovoid 1st flagellomere having long fine white cilia on apex. Arista (length unknown) thin, with fine, sparse and rather short cilia.

Thorax (Figs 29, 32) narrow, ochreous to yellow; pronotum with darker postpronotal area; most of mesonotum ochreous, with small pale spots behind humeral (postpronotal) callus and with a larger pale semicircular medial prescutellar one. There is a short, very narrow brown anteromedial stripe. Pleural part of thorax ochreous, with paler (whitish yellow) posterior half of mesopleuron (including its posterior triangular part) and metanotum. Thoracic chaetotaxy rich, with long but very fine setae: 1 hu and several short setulae on



Figs 27–28. *Homalomitra* sp., male (Brazil). 27 – genitalia laterally; 28 – aedeagal complex laterally (both figures after Mourgués-Schurter, 1987). Scale: 0.1 mm.

humeral callus; 3–4 dc macrosetae (1–2 presutural; the prescutellar very long) and 1–2 additional setulae in front and between them; ac short and restricted to prescutellar area; 2 npl (anterior strikingly longer than posterior); 2–3 posthumerals (all short and weak); 1 very long ?ia; 1 short sa; 1 longer pa; no prescutellar setae between pa and dc. Scutellum small, relatively narrow and apicaly rounded, with 1 pair of short thicker apical sc, and



Figs 29–33. *Homalomitra ecitonis* Borgmeier, female holotype (29, 30, 32), male (Brazil) (31, 33). 29 – head and thorax dorsally; 30 – head frontally; 31 – male f_1 and f_2 and f_3 – head and thorax laterally; f_3 – armature of male f_4 anteriorly. Scales: f_3 – 0.1 mm; others – 0.3 mm.

with 1 very reduced, hair-like lateral sc. No macrosetae on thoracic pleura. Propleuron bare. Mesopleuron with microsetulae on most of its anterior part and on posterodorsal stripe. Sternopleuron with microsetulae only dorsally and also most of pteropleuron covered with microsetulae. Hypopleuron bare.

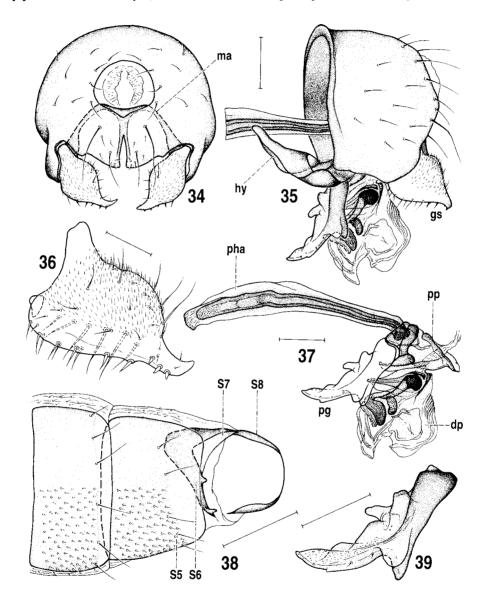
Legs long and robust in comparison with thorax size, pale ochreous and densely uniformly setulose. cx_1 (Fig. 32) unusually long as are also all tarsi. f_1 ventrally (Fig. 31) with a row of 7 short thickened setae (3 proximal anteroventral, 4 distal posteroventral); t_1 (Fig. 33) with only one ventral row of 8 thickened setae in central third of tibia and with a short ventroapical seta. f_2 simply densely setulose; t_2 with a pair of small ventropreapical setae. f_3 and t_3 uniformly densely haired. All tarsi robust, long, with strongly widened and dorsoventrally flattened segments, only the longer fore and mid basitarsus less dilated. Last segment of tarsi with excavated apex as typical for the genus. Mid basitarsus relatively short, ratio t_2 : $mt_2 = 2.43$. Hind basitarsus less flattened, more robust but shorter than next segment.

Wing (Fig. 41) long and relatively narrow, with veins and membrane ochreous to pale yellowish brown. C basally with a long and thin costagial seta; C strongly dilated in Cs_2 (its largest width almost twice that of marginal cell r_1) and distinctly produced beyond apex of R_{4+5} . Sc reduced, short. R_1 short; R_{2+3} long, very slightly sinuate and apically upcurved to C. R_{4+5} almost straight, only its apex bent to C. Cross-vein r-m very reduced, situated in basal fourth of wing. Discal cell (dm) very long and narrow, with long apical sector of M and shorter (less than half of the latter) that of CuA_1 , A_1 strongly reduced, very short. Cilia on posterior margin of wing probably long but lost in all specimens examined. Alula small, reduced. Wing measurements: length 1.75 mm, width 0.64 mm, Cs_2 : Cs_3 = 2.17, rm\dm-cu : dm-cu = 7.10. Haltere conspicuously long and slender, pale yellowish, with thin stem.

Abdomen ochreous brown, broader than in *H. antiqua* sp. n., hardly flattened. T1 dorsomedially membranous but dark margined laterally and posteriorly, and coalesced to T2. T2–T5 large, all with broad posterior pale and non-setulose margin. T2 and T5 long, almost as long as wide, the latter longer; T3 and T4 shorter, transverse. All terga densely finely setulose and T4–T5 with long thin setae in front of posterior bare margin; macrosetae in similar position in T2–T3 shortened and flattened. No remnants of S1 observed. S2 and S3 shorter and narrower than associated terga, both densely setulose and without long setae. S4 and S5 similar in size and shape to relevant terga but with shorter posterior bare margin, both densely setulose and with 6 long posterior setae. S6–S8 fused together, asymmetrical and strongly sclerotized, dark brown, almost bare. S6 ventrally with a pair of short digitiform posterior processes (Fig. 38).

Genitalia (Figs 34–37). Epandrium distinctly shorter and narrower than that of *H. antiqua* sp. n. or *H. albuquerquei*, and, in contrast to them, sparsely setulose, with longer but thin setae only around small rounded anal fissure and (2 pairs) on reduced cerci forming subanal plate. Subanal plate with usual narrow ventromedial cleft (Fig. 34). Hypandrium (Fig. 35) relatively robust, V-shaped, without medial rod-like apodeme. Medandrium (Fig. 34) simple and broad; its lateral arms connected with posterodorsal process of gonostylus. Gonostylus (Fig. 36) relatively broad and short, posteroventrally projecting in a pointed and somewhat internally bent corner. Micropubescence covering most of gonostylus but not entire external side as in *H. albuquerquei*; setae on gonostylus rich and rather long

(mainly on inner side) but shortened at anteroventral margin and some (in front of pointed apex) modified to short thick spines. Aedeagal complex robust (Fig. 37). Phallapodeme long and with distinct dorsal keel like that of *H. albuquerquei*. Phallophore with small epiphallus and dorsally (near its contact with phallapodeme) of complex structure.



Figs 34–39. *Homalomitra ecitonis* Borgmeier, male (Brazil). 34 – external genitalia caudally; 35 – genitalia laterally (apex of phallapodeme omitted); 36 – gonostylus sublaterally (widest extension); 37 – aedeagal complex laterally (postgonite not dotted); 38 – end of abdomen ventrally (genitalia removed); 39 – postgonite laterally. Scales: 36 – 0.05 mm, 38 – 0.3 mm; others – 0.1 mm.

Distiphallus robust, membranous in distal half and with complicated sclerotized structures dorsally having similar dark "core" as in *H. antiqua* sp. n. Postgonite (Fig. 39) large, very rich in various anterior and posterior projections and flat keels and with apex pointed. Ejacapodeme not observed, probably small.

FEMALE. Similar to male except for the following. Total body length about 2.5 mm (Borgmeier, 1931 gave the total length 3.34 mm but this was obviously based on a macerated specimen). f_1 and t_1 simply setulose, without special ventral setae. Wing measurements: length 2.14 mm, width 0.81 mm, Cs_2 : $Cs_3 = 2.23$, rm\dm-cu: dm-cu = 6.08.

Abdomen (Fig. 42) with only segments 1–3 similar to those of male. T2–T4 posteromedially with shortened and flattened setae. T3–T5 short and transverse, the latter with long macrosetae at posterior margin. S2 as in male and like S3 without macrosetae. S4–S6 similar to associated terga but with sparser setae (all long and thin) in front of posterior margins, longest setae having about half length of the relevant sternum.

Postabdomen (Figs 43, 44). Sclerites of 6th segment similar in structure and setosity (including dense microsetulae) to preceding ones but longer and narrower. T7 and S7 similar, posteriorly tapered, with a row of longer setae at posterior margin and several setulae scattered on disc. T8 much narrower than T7 but broader than S8, with only 6 setae in front of posterior bare margin. S8 smaller than T8, with a number of discal setulae in addition to posterior submarginal setae. Internal vaginal structures not studied because they are damaged in the specimens examined, probably largely membranous. Spermathecae (1+1) dark (originally blackish), not perfectly spherical (Figs 40, 45), with slightly protruded vertex. Sclerotized terminal part of duct about as long as diameter of spermatheca and provided with a crown of several tubercles at its insertion to spermathecal body. T10 very pale, narrow, posteriorly tapered and bearing a pair of dorsal setae. S10 (Fig. 44) essentially broader than T10, with a few setulae at posterior margin and, in contrast to S8, without micropubescence. Cerci small (Fig. 43), without micropubescence; all long hair-like setae broken off in the specimens available. Probable arrangement of setae indicated in Fig. 43.

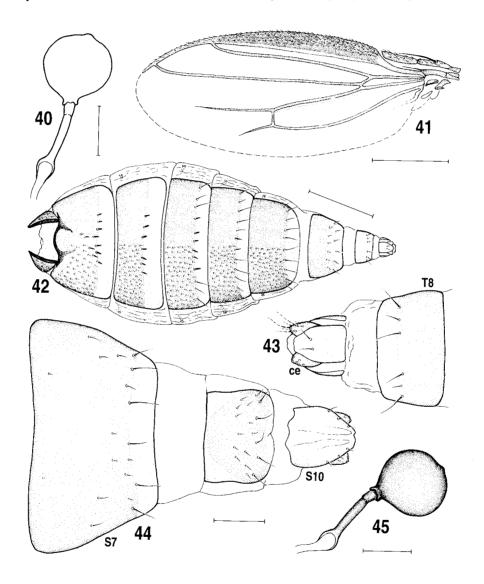
TYPE MATERIAL: Holotype ♀, labelled: "Campinas Goiaz, Schwarzmaier" (obverse, printed), "20.I.1930, E. preadator mataburro!" (reverse of the same label, handwritten) "Homalomitra ecitonis ♀ Holotypo, Campinas. Goyaz" (handwritten by Borgmeier). The specimen was dissected by T. Borgmeier and its left wing and left fore, mid and hind leg mounted in Canada balsam in 4 slides labelled "Homalomitra ecitonis ♀ Holotypo, aza", same but "pata anterior", "pata média" and "pata posterior" (all handwritten by Borgmeier). All four slides are deposited in MZSP (examined) but the actual specimen (without above extremities), mounted on minutia pin, is in USNM (examined). Abdomen of the holotype was removed and cleared (probably by G. Steyskal, see Steyskal, 1971) and preserved in glycerine. It is in poor condition and is now mounted in a coalesced plastic tube pinned below the specimen.

OTHER MATERIAL EXAMINED: Brazil: "Campinas, 1♂ 14.xi.1937", "praedator" (no collector); genit. prep. (USNM). "Nova Teutônia, 27°11′8″S, 52°23′W, 1♀ xii.1952, 300–500 m, Fritz Plaumann leg."; genit. prep. (MZSP).

DISTRIBUTION. Brazil.

BIOLOGY. *H. ecitonis* was found to be associated with doryline ant *Eciton (Labidus)* praedator F. Smith (Formicidae) already by Borgmeier (1931). This fact is also confirmed by the single true male of this species available. Specimens examined were taken in November, December and January (the holotype was collected on 20.i. not 22.i. as Borgmeier, 1931 stated, or 22.ii. as given by Mourgués-Schurter, 1987).

DISCUSSION. Homalomitra ecitonis forms together with H. tenuior sp. n. and H. albuquerquei the monophyletic sister-group to H. antiqua sp. n. This group is characterized by the following synapomorphic features: shortened apical sc; no ppl; no mspl; no stpl; no ptpl; male S6 with somewhat swollen and modified (processes, emargination) ventral medial part; female T7 and S7 with reduced setosity. H. albuquerquei clearly is the most



Figs 40–45. *Homalomitra ecitonis* Borgmeier, female holotype. 40 – spermatheca; 41 – wing; 42 – abdomen dorsally (setae on cerci missing); 43 – apex of postabdomen dorsally (setae on one cercus reconstructed); 44 – ditto ventrally (+ 7th segment; setae on cerci missing); 45 – spermatheca. Scales: 40, 45 – 0.05 mm; 41, 42 – 0.5 mm; others – 0.1 mm.

closely allied species to *H. ecitonis* (see discussion under that species below). *H. ecitonis* can be best recognized based on the above key.

Mourgués-Schurter (1987) redescribed *H. ecitonis* and was the first to illustrate its male genitalia and spermathecae. However, only the figure of the latter actually pertains to the species whereas the male genitalia she figured probably belong to an undescribed species or to *H. tenuior* sp. n. (see comments under *Homalomitra* sp. above). Thus, the true male of *H. ecitonis* is here described for the first time.

Homalomitra albuquerquei Mourgués-Schurter, 1987

Homalomitra albuquerquei Mourgués-Schurter, 1987: 116.

Description. Male. Total body length 2.34 mm (according to Mourgués-Schurter, 1987); general colour dark, black-brown. Head (heavily damaged, and, therefore, inadequately described) similar to that of *H. ecitonis* but much darker, black-brown. Interfrontalia indistinct, number of ifr non-recognizable. Cephalic chaetotaxy: 1 short oc; 1 distinct though short ors; 2 setae on vertex (1 exclinate = ?occe, 1 inclinate = ?occi or vti); vi relatively short; several setulae in a row behind it but no g. Gena, eye, face and antenna as in *H. ecitonis* but all dark, including brown antennae. Arista about as long as antenna, with relatively sparse and short cilia (as in *H. ecitonis*).

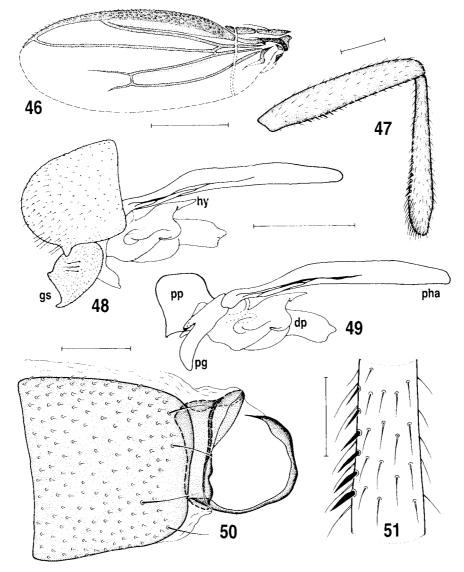
Thorax narrower than head, grey-brown to black-brown, including pleurons. Mesonotum somewhat paler posteriorly and on humeral callus. Thoracic chaetotaxy resembling that of *H. ecitonis*, including short apical sc. No macrosetae on pleural sclerites. Extent of mesopleural area covered by microsetae about the same as in *H. ecitonis*, i.e. larger than in *H. tenuior* sp. n. All pleural sclerites dark greyish brown, including posterior triangular part of mesopleuron, metanotum and postscutellum. Scutellum short, of the same shape and chaetotaxy as that of *H. ecitonis*.

Legs dark brown, long, somewhat more slender than in H. ecitonis. All coxae dark greyish brown. f_1 with 3–4 short, thickened anteroventral setae in basal third (Fig. 47); t_1 armed by a row of only 5–6 short, spine-like anteroventral setae between apical third and fifth (Fig. 51); apical fifth of t_1 ventrally densely finely haired. t_2 with 2–3 short subapical ventral setae, otherwise all femora and tibiae uniformly finely setulose. All tarsal segments dilated and dorsoventrally flattened but less than those of H. ecitonis; hind basitarsus and 2nd segment particularly hardly broader than following segments. Fore and mid basitarsus less dilated than subsequent segments. Ratio t_2 : $mt_2 = 2.72$.

Wing (Fig. 46) unusually dark, with distinctly brownish membrane and brown veins. C conspicuously incrassate in Cs_2 , almost filling cell r_1 , and having broad non-setulose posterior margin. Costagial seta well developed. R_{2+3} distinctly sinuate, apically attached to dilated part of Cs_2 . R_{4+5} very slightly sinuate, with apex distinctly upcurved to C. Discal (dm) cell long; apical sector of M markedly longer than that of CuA_1 . A_1 strongly reduced. Alula small, narrow. Marginal cilia not observed, probably lost. Wing measurements: length 1.75 mm, width 0.67 mm, Cs_2 : $Cs_3 = 2.55$, rm\dm-cu: dm-cu = 7.55. Haltere long, slender, with pale brown stem and long, brown knob.

Abdomen originally probably brown to dark brown, now (cleared by L. Mourgués-Schurter) pale ochreous brown. Both terga and sterna well sclerotized. T1 largely coalesced with T2, the latter large and long, conspicuously longer than T3 and T4 being distinctly transverse. T5 the largest tergum, longer than T2, posteriorly somewhat tapered and

its hind corners rounded. T2–T4 with longer setae only in posterior corners, posteromedially only with several small, somewhat thickened setulae. T5 with 6 (3 pairs) long setae in front of posterior margin and 1 pair medially in front of them. All preabdominal terga with microsetulae covering most of their discs except for the usual broad posterior margin. S2 and S3 anteriorly narrowed, posteriorly widest. S2–S4 subequal in lenth, thus, S2 shorter



Figs 46–51. *Homalomitra albuquerquei* Mourgués-Schurter, male holotype. 46 – wing; 47 – male f_1 and t_1 anteriorly; 48 – genitalia laterally; 49 – aedeagal complex laterally; 50 – apex of abdomen ventrally (genitalia removed); 51 – armature of male f_1 and t_1 anteriorly. Figs 48 and 49 after Mourgués-Schurter (1987). Scales: 46 – 0.5 mm; 51 – 0.1 mm; others – 0.2 mm.

than T2 and S3–S4 longer than T3–T4. S5 (Fig. 50) very long, similar to T5. All preabdominal sterna with 2 pairs of long setae in front of posterior margin; setae on S2 and S3 shorter, those on S4 and S5 longer; microsetulae on sterna denser than those on terga. Ventral part of S6 (Fig. 50) larger than in *H. ecitonis*, without projecting tubercles but with swollen, heavily sclerotized, characteristically emarginate posterior margin.

Genitalia. (Figs 48, 49, based on Mourgués-Schurter, 1987: Figs 3, 4). Epandrium long, with rather dense and short setae. Cerci and subanal plate not visible on Fig. 48, and, therefore, cannot be described. Hypandrium probably V-shaped, in Fig. 48 not distinguished from distiphallus or omitted entirely. Gonostylus (Fig. 48) with projecting and interally bent posteroventral corner, externally covered by dense micropubescence and bearing only a few setae. Phallapodeme long, robust, with well developed dorsal keel. Distiphallus not adequately figured, lacking enough detail. Postgonite (Fig. 49) distinctly different from that of *H. ecitonis*, with simple posterior digitiform projection and anteriorly curved apex. No further detail of the male genitalic structures are available.

Type material: Holotype & labelled: "Costa Rica, F. Nevermann" (obverse, printed), "3.XII.36, Nest praedator" (reverse of the same label, handwritten), "Homalomitra, b. E. praedator!, det. Borgmeier", "Homalomitra, Holotipo &, Det: L. Mourgués-Sch." (obverse), "Asa, e pernas e genitalia on lamina" (reverse of the same label) and "Homalomitra albuquerquei Mourgués-Schurter, J. Roháček des. 1997, Holotypus &" (red label). The specimen was originally preserved in ethanol, dissected and heavily damaged by L. Mourgués-Schurter who removed one wing, one of each pair of legs and genitalia and mounted them on two Canada balsam slides labelled "Homalomitra albuquerquei Holotipo, asa" (1st slide) and "Homalomitra albuquerquei Holotipo, pernas 1ª E, 2ª E, 3ª D, Gen." (2nd slide) and both "Holotypus &" (red label). The preserved remnants of specimen are now placed in coalesced plastic tube with glycerine pinned on the same pin as dried (done by senior author) worker specimen of host ant (all examined, deposited in MZSP).

Note. Unfortunately, both slides prepared by L. Mourgués-Schurter are extremely poor, with genitalia destroyed completely and, hence, unavailable for redescription. Therefore, original figures of genitalia by Mourgués-Schurter (1987) have to be used here.

DISTRIBUTION. Costa Rica.

BIOLOGY. The holotype (single known specimen) was found in a nest of the ant *Eciton* (*Labidus*) *praedator* F. Smith in December; thus it is associated with the same host species as *H. ecitonis*.

DISCUSSION. Homalomitra albuquerquei is most closely related to H. ecitonis Borgmeier and form with it a sister-pair diagnosed by the following features: arista shortly and sparsely ciliate; occiput without convex, pale and bare spot behind ocellar triangle; mesopleuron with large area covered with microsetae; similar chaetotaxy of male f_1 and t_1 ; C strongly dilated and with bare posterior margin in Cs_2 ; male S6 ventromedially thickened and modified. It can be easily distinguished from all known congeners (including H. ecitonis) by very dark body, legs and wings and by extremely dilated C in Cs_2 (almost completely covering marginal cell r_1). Further differences from H. ecitonis are listed in the key and the above description (viz. detailed armature of male f_1 and f_2 ; longer male S5; shape of male S6, gonostylus, postgonite etc.).

Genus Sphaeromitra gen. n.

Type species: Sphaeromitra inepta sp. n.

DIAGNOSIS. (1) Head (Figs 53, 55) long, as broad as thorax, dorsally slightly convex. (2) Frons very large and broad, anteriorly tapered. (3) Frontal triangle only indicated and

ocelli absent. (4) Interfrontalia and ocellar triangle absent; frons with 3 prominent protuberances in place of ocellar triangle. (5) Gena (Fig. 52) wide and less deep; occiput and postgena normal. (6) Frontal macrosetae absent completely; frons with microsetulae only. (7) Vibrissal angle well developed; face less oblique. (8) vi short but distinct; g absent. (9) Antennal scape (Figs 53, 55) distinctly enlarged but smaller than pedicel; scapes widely separated medially; pedicel slightly shorter than 1st flagellomere. (10) Arista apical, with dense and long haires. (11) Epistoma (Figs 52, 55) expanded dorsally and forming together with concave face deep antenal pits. (12) Maxillary palp dilated, relatively large (Fig. 55).

(13) Thorax (Fig. 53) not particularly narrow but relatively short; scutellum short but broad. (14) Thoracic chaetotaxy extremely reduced both on mesonotum (no macrosetae) and pleuron (1 small ppl, 1 short posterodorsal, and 2–3 longer posteroventral stpl). (15) No hu, posthumerals, npl, sa, pa (only very few and reduced microsetulae). (16) No ia. (17) No dc (only a sinuate row of microsetulae). (18) No sc, scutellum with scattered microsetulae only. (19) Mesopleuron not only divided but its posterior part completely membranous (Fig. 52); also ventral part of mesopleuron, most of sternopleuron (except for posterior and dorsal margin) and metapleuron (laterotergite) membranous. (20) Sclerotized part of mesopleuron, dorsal part of sternopleuron and pteropleuron with microsetulae. (21) Legs (Fig. 52) robust but short, with laterally compressed and widened femora (slightly) and tibiae (strongly). (22) Male f_1 and t_1 (Fig. 54) with a few anteroventral spine-like setae, including one long curved seta; all other femora and tibiae (including female f_1 and t_1) without macrosetae. (23) All tarsi with dilated and dorsoventrally flattened segments. (24)

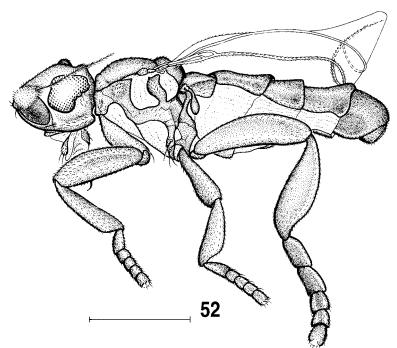
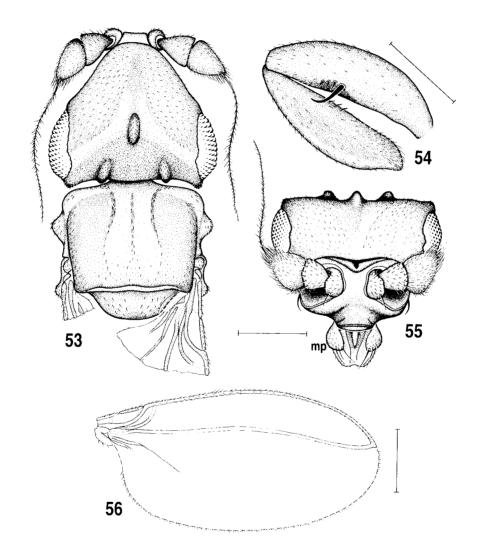


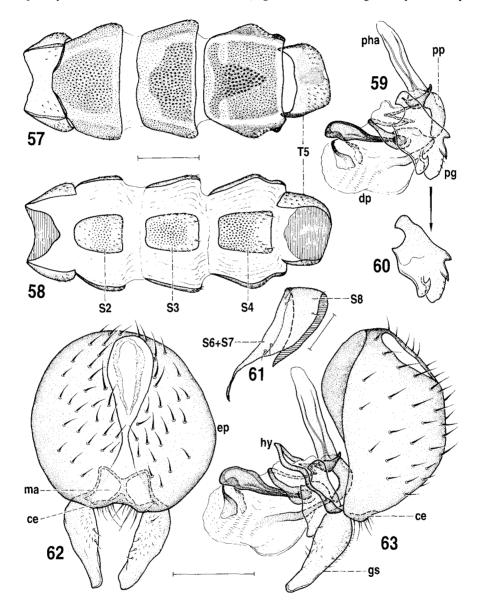
Fig. 52. Sphaeromitra inepta sp. n., male holotype. Scale: 0.5 mm.

Claws inserted in deeply excavated apical tarsal segment. (25) Wing (Fig. 56) short and broad, with short marginal cilia. (26) C without long costagial seta. (27) C slender and ending at apex of R_{4+5} . (28) Index Cs_2 : Cs_3 extremely small, less than 0.1, because of unusually shortened R_{2+3} . (29) Cell br, dm, and all cross-veins absent. (30) M absent, indicated by mere fold; CuA_1 short and cross-vein dm-cu not developed. (31) bm and cup cells not developed. (32) A_1 yet more reduced than in *Homalomitra*, with only short basal remnant developed. (33) Alula very small and narrow. (34) Haltere normal in size.



Figs 53–56. Sphaeromitra inepta sp. n., male holotype. 53 – head and thorax dorsally; 54 – male f_1 and t_1 anteriorly; 55 – head frontally; 56 – wing. Scales: 56 – 0.3 mm; others – 0.2 mm.

(35) Abdomen shorter, with large preabdominal terga but with reduced (narrowed) preabdominal sterna (Figs 57, 58). (36) Preabdominal terga and sterna without long setae at posterior margins and covered by short, scale-like microsetulae. (37) Male S5 (Fig. 58) completely absent. (38) Male S6, S7 and S8 (Fig. 61) coalesced together; particularly S6



Figs 57–63. Sphaeromitra inepta sp. n., male holotype. 57 – abdomen dorsally; 58 – ditto ventrally (genitalia removed); 59 – aedeagal complex laterally; 60 – postgonite laterally; 61 – 87 – 87 and 87 laterally; 87 – external genitalia caudally; 87 – genitalia laterally. Scales: 87, 87 – 87 mm; others – 87 mm.

and S7 completely fused and reduced, forming a band-like sclerite. (39) Epandrium (Figs 62, 63) of medium length, simple, without ventrolateral cleft. (40) Anal fissure of epandrium small, elongately ovoid. (41) Hypandrium reduced, strip-like, V-shaped in dorsal view. (42) Subanal plate (reduced cerci) fused with epandrium but medially below anal fissure desclerotized and ventrally bent, without long narrow ventromedial cleft. (43) Medandrium (Fig. 62) simple and small, weakly sclerotized. (44) Gonostylus unilobate, weakly sclerotized, with reduced micropubescence and setae. (45) Phallophore (Fig. 59) simple, short, without epiphallus. (46) Distiphallus short and robust, largely membranous but with slender internal sclerites arising from heavily sclerotized central "core" lying in its proximal part. (47) Postgonite (Fig. 60) robust but short, with various projections and keels. (48) Ejacapodeme very reduced or absent (not observed).

(49) Female postabdomen (Figs 64–66) with T6 and S6 different from preceding sclerites both in shape (much longer) and chaetotaxy (without scale-like microsetae). (50) T7 strikingly longer than S7 and both very different from T8 and S8 respectively. (51) T8 short, with longer setae than T7. (52) S8 short, narrower than T8, simple suboval, with dense micropubescence besides longer thin setae. (53) Spermathecae (1+1) black (Fig. 67), more or less sphaerical, with sclerotized part of duct unarmed but completely coalesced with body of spermatheca. (54) T10 and S10 (Figs 64, 66) without micropubescence. (55) Cerci with rich setosity but without micropubescence.

ETYMOLOGY. The name of the genus is an abbreviated conjunction of Sphaero[cera] + [Homalo]mitra and refers to its external similarity to both these unrelated genera; gender feminine.

DISCUSSION. The genus Sphaeromitra gen. n. is yet more odd than Homalomitra, resembling members of Sphaerocerinae not only by shape of its head and reduced setosity but also by similarly dorsally expanded epistoma, scutellum and preabdomen without setae, swollen legs (femora and tibiae) and reduced preabdominal sterna. However, all these similarities are only superficial as the analysis of the male and female postabdominal structures clearly demonstrated that it is related to Homalomitra despite many striking differences. Actually, Sphaeromitra is the more aberrant genus (see e.g. its unique wing venation, frontal structure of head, reduced pleural sclerites etc.) which accumulates many derived characters while *Homalomitra* represents its more ancient sister-group. Synapomorphic characters shared by both these genera are enumerated above in diagnosis of Homalomitrinae and also discussed below in the chapter "Phylogenetic considerations". Autapomorphic characters of Sphaeromitra are thought to be the following: 4, 6, 11, 14, 15, 17, 18, 19, 28-30, 33, 35-37, 49 and 50. Some of these are very striking and do not have any analogy in the whole family Sphaeroceridae, e.g., frons with 3 bulging protuberances instead of ocellar triangle; strongly reduced pleural sclerites (mesopleuron, sternopleuron, metapleuron); unusual hyaline wing with strangely reduced veins (R_{2,3} shortened and upcurved, M and all cross-veins absent etc.); peculiar dark, scale-like microsetulae on vertex of head (very minute) and preabdominal sterna (larger) and terga (largest in T4); male S5 completely absent; conspicuously reduced female T7 and S7; etc.

The genus includes only the type species, S. inepta sp. n. (Peru), described below.

Sphaeromitra inepta sp. n.

DESCRIPTION. Male (Fig. 52). Total body length 1.9 mm; general colour ochreous to pale brown, preabdominal terga and bulging protuberances on frons and vertex dark brown.

Head large and long (Figs 53, 55), as broad as thorax, very slightly convex on frons but strongly anteriorly tapered and, therefore, its dorsal outline roundedly triangular. Frons very large; its anterior half yellow, posteriorly darker ochreous to brown on vertex, all finely microtomentose (greyish to yellowish white) and dull. Frontal structures hardly recognizable; ocellar triangle, ocelli and interfrontalia absent; frontal triangle and orbits only indicated. Instead of ocellar triangle there are 3 prominent, laterally somewhat compressed, bulges on vertex and 1 additional (similar but smaller) tubercle in dorsal postocular position, all being darkened and covered with dark microsetulae. Cephalic chaetotaxy: no macrosetae except for a well developed vi and a ventrally directed seta on ventral margin of antennal scape; frons with numerous scattered microsetae as is also lower (darker) half of gena; area between bulges and tubercles on vertex and themselves covered by reduced, scale-like microsetulae. Genal height about half of the longest eye diameter; lower part of gena ochreous and setulose, its upper half pale yellow and as postgena bare. Vibrissal angle well developed and meeting with extremely expanded epistoma forming together with concave face deep, ovoid antennal cavities (Figs 52, 55). Eye reduced although larger than in Homalomitra spp., with somewhat reniform outline. Antenna yellow, with enlarged scape (although not as strongly as in *Homalomitra*) carrying a peculiar ventral seta; pedicel shorter than 1st flagellomere and finely microsetulose like scape; 1st flagellomere ovoid with conical apex and very dense and long (particularly apically) white ciliation. Both scapes separated by a broad bare band being as broad as scape (see Fig. 55). Arista apical, 1.8 times as long as antenna, rather densely and long ciliate. Palpus larger than that of Homalomitra, dilated and provided with 2 longer and several short setulae (Fig. 55).

Thorax (Figs 52, 53) with paler pleurons and darker mesonotum, both with extremely reduced setosity. Humeral callus (postpronotal lobe) yellow, with only 3 microsetulae. Mesonotum darker, ochreous brown laterally and pale ochreous medially, with a medial dark line in anterior two-thirds. There are 2–3 rows of black microsetulae in notopleural to postalar area, 1 dorsocentral row and 1 (single) medial row of ?acrostichal microsetulae. Scutellum short, wide and transverse, posteriorly rounded, with a number of microsetulae on both sides of disc. Pleural part of thorax very peculiar (Fig. 52): Propleuron short but normally sclerotized, with 1 small ppl. Mesopleuron with desclerotized (whitish membranous) anteroventral (above fore coxa) and posterior (corresponding to triangular area in *Homalomitra*) parts but with strongly bulging remaining sclerite being covered by black microsetulae. Sternopleuron also largely membranous and whitish, with a reduced dorsal and posterior band-like sclerite carrying 1 short posterodorsal and 2–3 longer posteroventral stpl. Pteropleuron well sclerotized and also protruding and with a number of dark microsetulae; metapleuron, on the contrary, membranous.

Legs (Fig. 52) robust, dilated; femora somewhat, tibiae strongly laterally compressed (slightly blade-shaped, especially t_3); pale yellow, only femora, particularly in distal half, ochreous to ochreous-brown. cx_1 much shorter than in *Homalomitra*, sparsely and shortly setulose. f_1 and f_2 with conspicuous armature on anteroventral side (Fig. 54): f_1 in distal third with 1 strong curved and 3 short black spine-like setae opposed by a row of 4 short black spines in proximal half of f_2 . Ventroapical part of f_3 bearing fine golden-yellow hairs. Other femora and tibiae without special setae, uniformly covered by fine microsetae. Ratio f_3 : f_4 : f_4 : f_5 : f_7 :

somewhat longer, longer than apical segment, the latter distinctly excavated. Hind tarsus also with flattened and dilated segments but more robust, with basitarsus and 2nd segment subequal, largest and provided with a brush of golden-yellow hairs on posteroventral margin; remaining segments (3–5) of hind tarsus shorter but not transverse, all of about the same length.

Wing (Fig. 56) very unusual for the family, relatively broad, with conspicuously reduced venation. Membrane hyaline, veins yellowish hyaline. No costagial seta; C not produced beyond apex of R_{4+5} , densely haired along its entire length. Sc reduced, not discernible. R_1 short and strongly upcurved to C; R_{2+3} very similar to R_1 , yet stronger curved, short and ending close to R_1 . R_{4+5} long, distinctly sinuate, ending near apex of wing. M not developed, present as only a more or less distinct fold (not visible in slide preparations). CuA_1 distinct, ending far from wing margin. No trace of cross-veins. A_1 present as a very reduced, poorly visible remnant. Alula very small, with a few marginal cilia. Marginal ciliation of wing short. Wing measurements: length cca 1.45 mm, width 0.7 mm, Cs_2 : $Cs_3 = 0.04$. Haltere normal in size, with white-yellow stem and dirty yellow knob.

Abdomen (Figs 57, 58). T1 relatively large, but dorsally desclerotized and whitish yellow; its narrow lateral parts dark yellow, shortly microsetulose. T2 (longer) and T3 (shorter) with dark brown disc covered with flat scale-like microsetulae and with narrow, ochreous lateral parts covered with finer scale-like microsetulae and some normal marginal setulae. T4 with large dark brown dorsal part (pattern as in Fig. 57, with largest scale-like microsetae centrally) and also lateral parts dark brown, separated from the main part by yellow stripe. T5 narrower but more extended ventrolaterally and slightly asymmetrical, with only simple microsetulae, yellowish ochreous with dark spots laterally and a small pale brown spot dorsomedially. S2-S4 narrow (Fig. 58); S2 whitish yellow with sparse fine microsetulae, S3 yellow with larger scale-like microsetulae and S4 ochreous with largest scale-like microsetulae; S3 and S4 with several normal setulae including 1 stronger in posterior corners in addition. S5 completely absent! Pleural membranous part of abdomen enlarged (because of reduced sterna), longitudinally wrinkled and whiteyellow. Postabdominal sclerites reduced (see Fig. 61), particularly S6 and S7 which are coalesced (as indicated by 2 pairs of setae) and form a short, band-like, strongly asymmetrical sclerite on left side of postabdomen. S8 also relatively short, slightly asymmetrical and situated dorsally.

Genitalia (Figs 59–63). Epandrium (Figs 62, 63) semispherical, lateroventrally brown, dorsally pale ochreous to yellow, with numerous short setae being denser posteriorly. Anal fissure (Fig. 62) shifted unusually dorsally and subanal plate below it long but largely membranous medially, with reduced cerci bent ventrally. Cerci with several fine pale setae. Medandrium distinct but small and weakly sclerotized, connected with posterodorsal corners of gonostyli. Hypandrium reduced, forming a very thin V-shaped strip (Fig. 63). Gonostylus (Figs 62, 63) pale yellow, weakly sclerotized, relatively small and slender, with blunt apex and several setulae at anterior and posterior margins and with some micropubescence restricted to dorsal half of posterior side. Aedeagal complex (Fig. 59) voluminous compared to epandrium but largely membranous although of complex structure. Phallapodeme short, simple and weakly sclerotized except for its dilated base. Phallophore relatively short, simple, crescent-shaped, without epiphallus. Distiphallus membranous except for dorsal sclerotized strips connected with phallophore, central, transversely oval (in

dorsal view) "core" and strongly clubbed, anteriorly directed sclerite arising from the latter. Anteroventral portion of distiphallus with some micropubescence arranged in 4 regular rows. Postgonite (Fig. 60) broad and complex, with curved anterior preapical projection, 2 pointed posterior thorn-like processes and blunt pale apex with some 3 subapical setulae. Ejacapodeme not observed.

Female. Similar to male unless mentioned otherwise. Total body length ca 2.2 mm. f_1 and t_1 without specialized armature, densely finely haired. Ratio t_2 : $mt_2 = 3.0$. Wing measurements: length ca 1.6 mm, width 0.8 mm, Cs_2 : $Cs_3 = 0.02$.

Abdomen with T1, T2 and S2 as in male but T3 and T4 are similar and resembling in shape and setosity male T3; also, S3 and S4 subequal and similar to male S3. T5 longer and darker than T4, of the same shape, colouration and chaetotaxy as male T4. S5 similar to male S4 (see above).

Postabdomen (Figs 64–66). T6 long and extended ventrally, with characteristic pigmentation (small central brownish spot dorsally, darker brown lateral markings, see Figs 64, 65) and finely densely microsetulose. S6 very narrow, tongue-shaped, with several setulae along lateral margins with the hindmost longest (Fig. 66). T7 long and narrow, posteriorly somewhat widened, largely membranous and very pale, with dark narrow lateral margins and lighther pigmented but setulose posterior margin (Fig. 64). S7 considerably shorter than T7 (Fig. 66), slightly shorter than broad, with narrowly darkly pigmented anterior margin and with 3 pairs of setulae posteriorly. T8 pale, short, distinctly transverse, slightly asymmetrical, with several longer setae (Fig. 64). S8 transversely oval, narrower than T8, with relatively long setae and dense micropubescence. Spermathecae (1+1) black (Fig. 67), with ball-shaped body and simple sclerotized part of duct completely fused with it (no boundary visible). T10 (Fig. 64) very weakly sclerotized, subtriangular, with acute posterior corner and a pair of very small dorsal setulae. S10 (Fig. 66) slightly broader than T10 and like the latter without micropubescence but with some scattered setulae. Cerci slender, attached to T10, with medium-long, hair-like setae and without micropubescence.

Type Material: Holotype δ , allotype 9 and paratype δ . "Peru: Madre de Dios, Zona Reserva Manu, Pakitza, 400 m, $11^{\circ}57'S$, $71^{\circ}17'W$, 18.-23.ii.1992, collected by B. Brown & D. Feener, Malaise trap #3". The holotype is intact, with only right wing removed; other specimens with genit. prep. Holotype and allotype deposited in DEBU, paratype in SMOC.

ETYMOLOGY. The species is named "inepta" (Lat. = inept, absurd; an adjective in nominative singular) because of its extremely strange appearance and many unusual features, unexpected in Sphaeroceridae.

DISTRIBUTION. Peru.

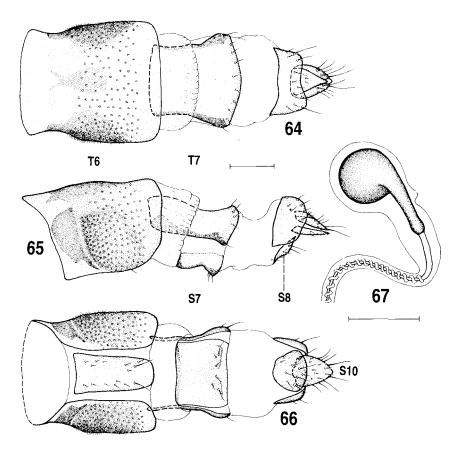
BIOLOGY. All three type specimens were collected in Malaise trap in February.

Discussion. The species is easily recognizable by many unique features mentioned above in the discussion under generic diagnosis. Its seeming similarity to species of Sphaerocerinae is only superficial; in fact all similar structures (including epistoma, reduced setulae, incrassate legs, narrowed preabdominal sterna) are different in detail.

PHYLOGENETIC CONSIDERATIONS

The relationships of Limosininae and Homalomitrinae are demonstrated by two, relatively weak, synapomorphies (see characters 1 and 2 in the cladogram, Fig. 68), both dealing with wing venation. Moreover, species of the subfamily Homalomitrinae possess the same, apparently plesiomorphic, type of the male external genitalia (epandrium simple, without ventrolateral cleft) as do all Limosininae. Therefore, Homalomitrinae cannot be

associated with the copromyzine clade (= Copromyzinae + Sphaerocerinae) the monophyly of which is based on the presence of epandrial cleft, nor with the recently established subfamily Tucminae (Marshall, 1996) because of the lack of the male 6th tergum (= a synapomorphy of all remaining subfamilies of Sphaeroceridae, except for Tucminae) as well as synapomorphies of that group (see Marshall, 1996). The monophyly of the Limosininae has not been unequivocally demonstrated (cf. also Marshall, 1997) and the subfamily may form a paraphyletic group composed of several clades, some of which will possibly have to be separated as higher taxonomic units in the future. Therefore, the subfamily Limosininae is treated here as only a somewhat generalized out-group of Homalomitrinae characterized by features i and ii (see Fig. 68), the polarities of which are uncertain. We suspect that two (1+1) spermathecae (known also in Tucminae, Copromyzinae and Sphaerocerinae) is the primitive state, and that the doubling of one of them (2+1; character ii) might either occur several times in Limosininae or could be a putative synapomorphy of the subfamily. If the latter alternative is correct, then some genera of Limosininae have the number of spermathecae secondarily reduced (to 1+1 or 2+0).



Figs 64–67. Sphaeromitra inepta sp. n., female allotype. 64 – postabdomen dorsally; 65 – ditto laterally; 66 – ditto ventrally; 67 – spermatheca. Scales: 67 – 0.05 mm; others – 0.1 mm.

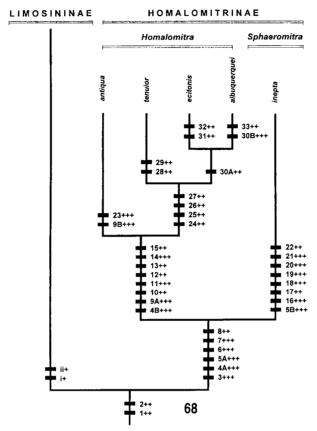


Fig. 68. Cladogram showing the inferred relationships of Homalomitrinae within the limosinine clade of Sphaeroceridae. Numbers refer to the following characters, (+), (++) and (+++) indicate character weighting based on subjective assessment of the likelihood of misinterpretation of homology or polarity. Unique characters considered to be strong evidence of synapomorphy are given the greatest weight and coded (+++). Characters marked A, B are postulated as transformation series.

Characters mentioned in the cladogram

Apomorphic condition (black rectangles) Plesiomorphic condition (not figured) i. Mid and hind tibiae and femora dorsally without i. Mid and hind tibiae and femora dorsally with at least some macrosetae. macrosetae. ii. Spermathecae 2+1. ii. Spermathecae 1+1. 1. M and CuA, not reaching wing margin; C ending 1. At least M reaching wing margin and C extended at or somewhat beyond apex of R_{4+5} . to its apex. 2. Cell bm absent. 2. Cell bm present. 3. Head long and very broad, dorsally flat; frons 3. Head normal, short and high; frons narower. large. 4A. Antennal scape very small. 4A. Antennal scape enlarged. 4B. Scape smaller than pedicel; scapes medially 4B. Antennal scape larger than pedicel; scapes separated. meeting medially.

- 5A. Mesopleuron divided, with posterior part less sclerotized.
- 5B. Mesopleuron with posterior part membranous; also sternopleuron and metapleuron partly membranous.
- 6. All tarsal segments dilated and flattened.
- 7. Claws in excavated apical tarsal segment.
- 8. Female T10, S10 and cerci without micropubescence.
- 9A. Gena narrowed (shortened); occiput enlarged.
- 9B. Gena narrower.
- 10. Maxillary palp very small.
- 11. 1 very long ?intra-alar seta.
- 12. Wing with long marginal cilia.
- 13. C with 1 long costagial seta.
- 14. Phallophore of complex structure.
- 15. Spermatheca with a crown of tubercles on scle- 15. Spermatheca with simple sclerotized part of rotized part of duct.
- 16. Frons with 3 prominent tubercles.
- 17. Epistoma expanded dorsally and forming deep antennal pits.
- 18. Mesonotum completely without macrosetae.
- 19. Cell br, dm, all cross-veins and M absent.
- 20. Male S5 absent.
- 21. Microsetae on abdomen modified to flat, short scales.
- 22. Female T7 much longer than S7 and both largely membranous.
- 23. Head longer and more compressed dorsoventrally.
- 24. Apical sc short ad thick.
- 25. No macrosetae on thoracic pleuron.
- 26. Male S6 with modified ventromedial part.
- 27. Female T7 and S7 with reduced setosity.
- 28. Anterior part of mesopleuron with large bare (without microsetulae) posterior area.
- 29. Female T7, S7 and S8 narrow.
- 30A. C conspicuously dilated in Cs₂.
- 30B. C extremely incrassate in Cs2.
- 31. Postgonite complex.
- 32. Male S6 ventromedially with 2 digitate
- 33. Male f, and t, with less numerous spine-like setae

- 5A. Mesopleuron undivided.
- 5B. Mesopleuron with more or less sclerotized posterior triangular part; sterno- and metapleuron well sclerotized.
- 6. Only hind basitarsus and 2nd segment thickened.
- 7. Claws on simple apical tarsal segment.
- 8. T10, S10 and cerci micropubescent.
- 9A. Gena and occiput normal.
- 9B. Gena broader.
- 10. Maxillary palp broader, clavate.
- 11. No ?intra-alar seta.
- 12. Wing with short marginal cilia.
- 13. C without long costagial seta.
- 14. Phallophore simple, compact.
- 16. Frons without tubercles.
- 17. Epistoma small, not expanded dorsally.
- 18. Mesonotum with rich macrosetae.
- 19. Cells br, dm, cross-veins and M present.
- 20. Male S5 present, long and large.
- 21. Microsetae on abdomen normal, hair-like.
- 22. Female T7 and S7 subequal, sclerotized.
- 23. Head shorter, less compressed.
- 24. Apical sc longer, thin.
- 25. Thoracic pleuron with macrosetae.
- 26. Male S6 simple ventromedially.
- 27. Female T7 and S7 densely setose.
- 28. Anterior part of mesopleuron largely microsetulose.
- 29. Female T7, S7 and S8 broader.
- 30A. C not strikingly dilated in Cs2.
- 30B. C dilated but less incrassate in Cs₂.
- 31. Postgonite simpler.
- 32. Male S6 ventromedially emarginate.
- 33. Male f, and t, with more spine-like setae.

In contrast to the Limosininae, the Homalomitrinae branch is well defined as a monophyletic lineage with a number of strong or even unique synapomorphies (see characters 3–8 in Fig. 68) within the whole of the Sphaeroceridae.

Interestingly, the two genera of Homalomitrinae, viz. *Homalomitra* and *Sphaeromitra* gen. n., represent very different and clearly monophyletic (see Fig. 68) lineages unrelated to subfamilies Copromyzinae and Sphaerocerinae (constituting the copromyzine clade) but conspicuously paralleling them superficially. *Homalomitra*, having rich and long setae on thorax and abdomen and broad preabdominal sterna, resembles Copromyzinae, whereas *Sphaeromitra*, possessing expanded epistoma, narrowed preabdominal sterna, modified microsetulae on head and abdomen and lacking mesonotal and abdominal macrosetae, imitates Sphaerocerinae. Such an enormous morphological diversity within the same clade supports the establishment of the subfamily Homalomitrinae.

The monophyly of *Homalomitra*, the more primitive of the homalomitrine genera, is well-documented by synapomorphies 4B, 9A, 10–15, although some of them are not unique within limosinine clade and, hence, of lower weight (e.g. 10 – reduced palp, 13 – long costagial seta); on the other hand, there are several strong synapomorphic features (e.g. 4B – very enlarged scape, 9A – narrowed gena and extended occiput, 14 – complex phallophore). The unsual, very long ?intra-alar seta (11) has obviously no analogy within the Sphaeroceridae and is treated here as a strong apomorphy, although there is another (less probable) interpretation possible, i.e. to consider it a plesiomorphic character lost in all other Sphaeroceridae.

Sphaeromitra gen. n., the sister-group of Homalomitra, accumulates numerous, highly derived characters, including 17 – expanded epistoma and deep antennal pits which evolved independently in parallel to certain genera of the Sphaerocerinae. Further unusual apomorphies involve 5B – extremely reduced pleural sclerites, 19 – strongly modified wing venation, and 20 – loss of male S5. The male genitalia, in contrast, are highly plesiomorphic and similar to those of Homalomitra, with yet more primitive (simple and compact) phallophore.

Within the *Homalomitra* clade, *H. antiqua* sp. n. is the most ancient species which forms the sister-group to all other known species. It is characterized by a number of plesiomorphic features, particularly in preservation of macrosetae on thoracic pleuron. The relationships of the remaining species of *Homalomitra* are shown in the cladogram (Fig. 68), with *H. albuquerquei* displaying maximal number of derived characters. There is an interesting transformation series of the thickness of costa, being relatively slender in *H. antiqua* sp. n., slightly dilated in *H. tenuior* sp. n., strongly broadened in *H. ecitonis* and extremely incrassate in *H. albuquerquei*.

COMMENTS ON THE BIOLOGY AND DISTRIBUTION

We know very little of the biology and distribution of these rarely collected flies, but what we know is intriguing. *Homalomitra* species have been repeatedly collected in association with one species of ecitonine ant, *Eciton* (*Labidus*) *praedator*. Adult flies have been taken "associated with workers" and at the nests, but we do not know if they were clinging to workers or just nearby (only Borgmeier, 1931 noted, that "the insect was walking in the middle of the ants"), we do not know if the nests are bivouacs or statatory phase nests, and we do not know how they were collected or what they were doing. The reduced

thorax and modified legs suggest that they might get around by phoresy rather than flight, but the records from Malaise and light traps suggest otherwise. Perhaps the larvae develop in ant kitchen middens, and the adults mate and oviposit in association with statatory nests.

Although our limited knowledge of the distribution of the Homalomitrinae is based on a few records from Costa Rica, Ecuador, Colombia, Peru and Brazil, species seem to have wide and overlapping ranges, with individual species occurring over wide geographic and ecological ranges. *Homalomitra antiqua* sp. n., for example, occurs in the cloud forest of Costa Rica and in Amazon lowland forest in Brazil, and the genus extends from southern Brazil to Costa Rica. Both the most derived (*H. albuquerquei*) and most primitive (*H. antiqua* sp. n.) species of the genus occur in Costa Rica.

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